

EFFECTS OF FOREST FRAGMENTATION BY AGRICULTURE ON AVIAN COMMUNITIES IN THE SOUTHERN BOREAL MIXEDWOODS OF WESTERN CANADA

KEITH A. HOBSON^{1,2} AND ERIN BAYNE^{2,3}

ABSTRACT.—Little is known about the effects of forest fragmentation on bird communities in the boreal forests of western North America. Assessing the impact of forest fragmentation on bird communities has been complicated by the fact that few studies have applied statistical analyses that account for the possibility that individuals are randomly dispersed within landscapes. From 1993–1997, we contrasted bird communities in contiguous forest (54 sites) and nearby forest fragments surrounded by agricultural land (106 sites, 0.2–123 ha). Species were divided into groups based on migratory strategy (resident, short-distance migrant, long-distance migrant, and irruptive) and edge-sensitivity (edge, edge-interior, and interior). For each group, we tested whether richness and abundance were different from what would be expected if birds were distributed randomly across landscapes. Species richness was higher than expected in contiguous forest for interior species, whereas edge and short-distance migratory species were more common in the fragmented landscape. Similarly, the total abundance of interior and long-distance migratory birds was higher in contiguous forest, whereas edge birds were more abundant in the fragmented landscape. Brown Creeper (*Certhia americana*), Swainson's Thrush (*Catharus ustulatus*), Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Blackburnian Warbler (*Dendroica fusca*), Black-throated Green Warbler (*Dendroica virens*), and Bay-breasted Warbler (*Dendroica castanea*) were virtually absent from the fragmented landscape, yet were common in contiguous forest. Within the fragmented landscape, forest fragment size had little effect on species richness but was significantly correlated with abundance of all migratory and edge-sensitivity groups except edge and short-distance migrants. Probability of occurrence, controlling for random placement, was positively correlated with forest fragment size, percent forest cover within 5 km, or the interaction between size and cover for 19 species, most of which were associated with forest interiors. Predation and brood parasitism were higher on nests of ground and shrub nesting birds in the fragmented landscape than in contiguous forest. Fragmentation of contiguous forest in the southern boreal mixedwood zone of western Canada has a negative impact on the abundance of several resident and long-distance migratory species. Received 23 Nov. 1999, accepted 6 May 2000.

The effects of anthropogenic fragmentation of forests and other habitats is one of the most pressing conservation issues currently facing avian and landscape ecologists (Temple and Wilcox 1986, Robinson et al. 1995, Faaborg et al. 1998). These issues have led to numerous studies on the effects of fragment size on the composition of avian communities. Species richness and the relative abundance of interior species are often positively correlated with forest fragment size (reviewed by Walters 1998). Other patterns that are emerging in North America relate to differential effects of fragmentation depending on the migratory status of birds. In particular, long-distance migrants seem to be less common in small forest fragments than short-distance migrants or res-

ident species (Lynch and Whigham 1984; Freemark and Merriam 1986; Askins et al. 1987, 1990; Robinson et al. 1995; Faaborg et al. 1998).

Despite the well-documented negative impacts of small fragment size on forest bird communities, the mechanisms causing this pattern remain unclear. In general, forest fragmentation seems to result in more nest predation and brood parasitism in landscapes fragmented by agriculture than in contiguous forest (Andr en 1995, Robinson et al. 1995). This has led to the suggestion that the reduced abundance or absence of species from small fragments is due to birds avoiding areas where rates of nest predation and brood parasitism are high (reviewed by Walters 1998). Increased predation or brood parasitism in small forest fragments may influence avian community structure by directly killing incubating or brooding birds, reducing recruitment through lower productivity, and/or increasing adult breeding dispersal (Haas 1998, Bayne 2000).

¹ Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, 115 Perimeter Rd., Saskatoon, SK, Canada, S7N 0X4.

² Dept. of Biology, Univ. of Saskatchewan, 112 Science Place, Saskatoon, SK, Canada, S7N 5E2.

³ Corresponding author; E-mail: Keith.Hobson@ec.gc.ca

That biotic processes such as nest predation are different in small versus large fragments does not necessarily demonstrate that such factors are the cause of species-area effects. Bird communities in small forest fragments may be a random sample from the regional species pool (Connor and McCoy 1979, Coleman et al. 1982, Møller 1987, Haila et al. 1993, Andrén 1996), such that species occur in fragments in proportion to the size of the fragment and the overall abundance of the species in the landscape (Freemark and Collins 1992, Hinsley et al. 1995). If birds show random dispersion, less common species should have a lower probability of occurrence in small forest fragments, and regionally abundant species should have similar abundance in most forest fragments regardless of size (Opdam et al. 1985). Clearly, determining whether species-area relationships are the result of random dispersion or are the result of non-random biotic differences, such as nest predation, is critical to avian conservation.

The objective of our study was to determine if species richness of different migratory and edge-sensitivity groups, and the abundance of individual forest bird species in different sized forest fragments in an agricultural landscape were different from what would be expected if birds were randomly distributed across the landscape. At a larger scale, we compared whether the distribution of birds was different between contiguous forest and forest fragments in an agricultural landscape, and whether nest success differed between these landscapes. We conducted this work in the southern boreal mixedwood forest of central Canada, an area with one of the highest levels of breeding avian biodiversity in North America (Robbins et al. 1989). These forests are naturally patchy because of fire, consisting of broad mosaics of stand types widely distributed across the landscape (Niemi et al. 1998). As a result of the patchy nature of the boreal forest, it has been suggested that birds breeding in the boreal forest might be able to tolerate a higher degree of fragmentation than birds in other ecosystems (Schmiegelow et al. 1996, Niemi et al. 1998). However, most work on the effects of forest fragmentation on boreal forest birds in Canada has been conducted in landscapes fragmented by industrial forestry. It remains unclear whether birds respond

to fragmentation by agriculture in the same way that they respond to fragmentation caused by fire or harvesting in the boreal zone.

METHODS

Study area and site selection.—Our study was conducted in the southern boreal mixedwood zone of north-central Saskatchewan in 1993, 1995, 1996, and 1997. Point counts in contiguous forest were conducted in Prince Albert National Park (NP), a 387,500 ha protected area surrounded by agricultural land and commercial forest (53° 57' N, 106° 22' W). Surveys in the fragmented landscape were conducted in the rural municipality of Paddockwood (53° 31' N, 105° 34' W), a 135,000 ha area of privately owned land, of which 70% is used for agriculture and 25% is forest fragments (see figure in Bayne and Hobson 1997). Forests in this area are dominated by white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*), with some black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*). The shrub layer is variable in density and composition with beaked hazelnut (*Corylus cornuta*), red-osier dogwood (*Cornus stolonifera*), green alder (*Alnus crispa*), and white spruce saplings the most common shrub species. Fire was the dominant disturbance regime in this area, with a pre-settlement fire interval of approximately 30 years. Subsequent fire suppression has since increased this interval to about 200 years (J. Weir, pers. comm.).

Sites were selected from 1:12,500 air photo maps based on their tree composition, age, isolation, shape, lack of disturbance (e.g., cattle grazing or selective timber harvest), and size. Sites were pure aspen, aspen-spruce mixedwoods, or pure white spruce stands. Approximately equal numbers of sampling stations were surveyed in each forest type and fragment size. All stands we surveyed were older than 50 years and fragments were completely isolated from other forest fragments by a field or pasture. On average, the minimum distance between neighboring patches was 54 ± 30 m. The minimum distance between patches, as estimated by the LANDSAT imagery, was 30 m. Distance between sampled patches was at least one kilometer. Sites in the fragmented landscape ranged from 0.2–123 ha. Control sites were chosen from forest inventory maps for Prince Albert National Park and were located in upland forests similar to those surveyed in the fragmented landscape.

Survey methods and environmental attributes.—We evaluated the relative abundance of bird species in each landscape using the Indices Ponctuel d'Abondance (IPA) point count technique (Blondel et al. 1970). The number of point count stations we established at a site (i.e., forest fragment or stand in contiguous forest) depended on size and shape of the site. Stations were selected *a priori* from air photos, with the goal of maximizing the number of stations per site. All sites had a maximum of five point count stations separated by at least 250 m. In all sites larger than 3

ha, stations were at least 100 m from any anthropogenic edge. In contiguous forest, we established 223 point count stations at 54 sites, while in the fragmented landscape we surveyed 202 point count stations at 106 sites. Sampling effort was not equal among years. Of the contiguous forest sites, 31 were sampled in 1993, 8 in 1995, 5 in 1996, and 10 in 1997. In 1993, 5 sites were surveyed in the fragmented landscape, 21 in 1995, 15 in 1996, and 65 in 1997. Each site was visited in only one year.

Each station was visited twice per season, once in late May or early June and once in late June. We used two observers each year and alternated observers between visits at each site. Between 04:00 and 09:30 CST, all birds heard or seen during ten minutes were recorded within approximately 100 m of each point count station. Counts were subject to the constraint that only birds estimated to be within the forest stand or fragment of interest were recorded. At each station, the maximum number of individuals of each species from both visits was used as an index of relative abundance. We excluded raptors and species that nest in wetland habitats. For statistical analyses, we included only species detected at 5% or more of the sites. All species were used when calculating species richness. When estimating species richness, we also categorized species by migratory status (irruptives, resident, short-distance, long-distance migrants) and edge-sensitivity (edge, edge-interior, interior). While these categories were somewhat arbitrary, they are useful for making comparisons with previous studies (Whitcomb et al. 1981, Ambuel and Temple 1983, Freemark and Merriam 1986, Blake and Karr 1987, Johns 1993, McCollin 1993).

At each station, we estimated the proportion of the canopy composed of coniferous species to the nearest 10%. Based on the average site values we classified each site as either a pure aspen (<25% conifer cover), mixedwood (25 to 75% conifer), or pure white spruce stand (>75%). We used LANDSAT Thematic Mapper satellite imagery taken in 1995 by the Prairie Farm Rehabilitation Agency to determine the size of each forest fragment and the percentage of the total land area that was forested within 5 km.

From 1996 to 1999, we monitored active nests of ground and shrub nesting passerines in seven forest fragments ranging in size from 5–40 ha, and five contiguous forest plots. All sites were located within mixedwood stands. We marked each nest we located with flagging tape, approximately 10 m from the nest. Nests were checked every 3 to 4 days, more often near fledging time. During each check, we recorded the number of eggs (host and cowbird), number of nestlings, and any disturbance to the nests.

Statistical analyses.—To determine whether observed species richness and total abundance of each edge-sensitivity and migratory group was greater than expected if birds were randomly distributed, we used rarefaction to estimate the mean number of species expected in sites that contained different number of point-count stations. Rarefaction estimates the number

of species expected from a given sample of point counts based on multiple random sampling of the original data (James and Rathbun 1981). In other words, we used rarefaction to determine how many more species would be expected in large sites simply because they were sampled more (i.e., had more stations) than small sites with only a couple of stations. Rarefaction estimates were calculated using the computer program EstimateS 5 (Colwell 1997). The expected number of species and total number of individuals per site as estimated by rarefaction was then subtracted from the observed number of species and total number of individuals per site, respectively. This provided an estimate of the departure from random (i.e., controlled species richness and abundance for increased sampling in larger patches).

A randomization procedure based on multiple linear regression modelling (Manly 1990) was used to determine whether the departure from random was influenced by landscape, year, forest type, and the interactions forest type \times landscape, and landscape \times year. The year \times forest type interaction was not examined because not all stand types were sampled in each year. All variables were entered into the model simultaneously. Randomization testing was also used for sites in the fragmented landscape to determine whether the departure from random was influenced by forest fragment size, forest cover within 5 km, forest type, year, and the interaction between size and cover. The significance of the main and interactive effects in each model was determined by randomly shuffling the original data 1000 times. The number of times the randomly shuffled data had a residual sums of squares greater than the observed data was used to determine the approximate probability value (Manly 1990). When the main or interactive effects were significant at $P < 0.05$, a randomization test based on the least significant difference procedure was used to determine which groups within factors were significantly different. The strength of randomization testing is that the underlying distribution does not have to follow any particular statistical distribution, nor do the data have to fit the assumption of homoscedasticity (Manly 1990). Randomization testing was done using the program PopTools (Hood 2000).

We also compared whether individual species were more or less abundant than would be expected if birds were randomly distributed. To determine expected abundance of individual species, we calculated the average abundance per point count station from all point count stations and multiplied this by the number of stations within each site. The observed abundance was the sum of all stations within a site. We calculated the departure from random for each species by subtracting the expected abundance from the observed abundance at the site level (Hinsley et al. 1996). Each species at each site was then classified as either having more individuals than expected (classified as 1) or fewer individuals than expected (classified as 0). Sites where observed abundance – expected abundance = 0 were classified as having fewer individuals than expected.

Logistic regression modelling was used to determine whether the proportion of sites where individual species were more abundant than expected was influenced by landscape, year, forest type, forest type \times landscape, and landscape \times year. We also used logistic regression modelling for sites in the fragmented landscape to determine whether the departure from expected was influenced by forest fragment size, percent forest cover within 5 km, size \times cover, forest type, and year. An all-possible regression procedure was employed where all combinations of the independent variables were examined. From all possible models, we selected the model that had the lowest Akaike Information Criteria (AICc) value. Models with the lowest AICc values explain the greatest amount of variation using the fewest number of variables (Burnham and Anderson 1998). AICc modelling was used instead of forwards or backwards stepwise logistic regression because these techniques can give different results depending on which parameter is entered or removed from the model first (Kleinbaum et al. 1988). When competing models had AIC values < 2 , we presented the model that had the fewest variables that were significant at $P < 0.10$. Logistic regression modelling was done in SPSS Version 9.

For each landscape, we calculated nest success using the Mayfield method (Hensler and Nichols 1981). Mayfield estimates weight the importance of each nest in the analysis based on the stage the nest was discovered and the number of days that nest was observed. Daily survival rate was estimated using the 50% mid-way assumption, where a nest was assumed to have fledged or been destroyed half way between subsequent visits. Mayfield estimates of daily nest success were compared among landscapes using the program CONTRAST, which utilizes a modified chi-square test (Sauer and Williams 1989).

RESULTS

Comparisons between landscapes.—The departure from random was higher than expected in the fragmented landscape relative to contiguous forest for richness of all species ($P = 0.03$), edge species ($P < 0.001$), and short-distance migrant species ($P < 0.001$; Table 1). Interior species richness was higher than expected in contiguous forest relative to the fragmented landscape ($P = 0.01$). Richness of edge-interior ($P > 0.05$), resident ($P > 0.05$), long-distance ($P > 0.05$) and irruptive species ($P > 0.05$) were no different between landscapes from what would have been expected if species were distributed randomly (Table 1). Forest type influenced species richness ($P = 0.01$), with the departure from random being higher in mixedwood than in trembling aspen and intermediate in white spruce. Resident ($P = 0.01$) and irruptive species ($P < 0.001$) had

higher than expected richness in white spruce and mixedwoods relative to pure aspen stands. Similarly, the departure from random was higher for edge-interior species in mixedwoods than in aspen or white spruce ($P = 0.03$). Mixedwood and white spruce stands had a higher departure from random for interior species richness than in trembling aspen. However, the interaction between forest type and landscape was significant for interior species richness ($P < 0.001$). Interior species richness was higher in contiguous forest than in the fragmented landscape for mixedwood and white spruce stands, whereas there was no difference in aspen stands. The departure from random for long-distance migrant richness was not influenced by landscape ($P > 0.05$), forest type ($P > 0.05$), or any of the two-way interactions. Year was not a significant predictor of the departure from random for species richness for any of the edge-sensitive or migratory groups.

The departure from random for total abundance was not significantly different between landscapes for all birds combined ($P > 0.05$), edge-interior ($P > 0.05$), resident ($P > 0.05$), short-distance migrants ($P > 0.05$), or irruptives ($P = 0.10$). The total abundance of edge birds was higher than expected in the fragmented landscape relative to contiguous forest ($P < 0.001$). Abundance of interior birds ($P = 0.003$) and perhaps long-distance migrants ($P = 0.07$) was higher in contiguous forest than in the fragmented landscape. However, the interaction between forest type and landscape was significant for interior species ($P = 0.02$). The abundance of interior birds was higher in contiguous forest than in the fragmented landscape for mixedwood and white spruce stands, whereas there was no difference between landscapes in aspen stands. Edge birds were more abundant than expected in aspen stands relative to mixedwood or white spruce ($P = 0.05$). Conversely, mixedwood and white spruce stands supported more interior ($P = 0.005$), resident ($P = 0.01$), and irruptive birds ($P < 0.001$) than pure aspen stands. Short-distance migrants were more abundant than expected in white spruce than mixedwoods or pure aspen ($P = 0.01$). Annual variation in abundance was observed for all birds ($P = 0.003$), edge-interior ($P = 0.02$), interior ($P = 0.003$), resident ($P =$

TABLE 1. Mean departure (least squares means) from what would be expected if birds were randomly distributed among landscapes and forest types for species richness and total abundance. Numbers in parentheses are the lower and upper bounds of the 95% confidence intervals for that estimate. Probability that departure from random was greater than expected is also given.

	Contiguous forest	Fragmented forest	P	Trembling aspen	Mixedwoods	White spruce	P
Departure from random for species richness							
All species	-5.9 (-7.3, -4.6)	-3.1 (-4.2, -1.9)	0.03	-5.9 (-6.9, -4.9)	-3.8 (-4.9, -2.8)	-3.8 (-5.6, -1.9)	0.01
Edge	-3.2 (-4.0, -2.6)	0.9 (0.3, 1.5)	<0.001	-0.4 (-0.9, 0.0)	-1.6 (-2.1, -1.0)	-1.7 (-2.6, -0.7)	0.19
Edge-interior	-1.5 (-2.1, -0.9)	-1.4 (-1.9, -0.9)	0.19	-1.8 (-2.3, -1.4)	-0.9 (-1.4, -0.4)	-1.6 (-2.4, -0.7)	0.03
Interior	-1.2 (-2.0, -0.3)	-2.6 (-3.2, -1.9)	0.01	-3.6 (-4.2, -3.0)	-1.4 (-2.1, -0.7)	-0.5 (-1.7, 0.6)	<0.001
Resident	-0.6 (-1.2, -0.1)	-0.6 (-1.0, -0.2)	0.92	-1.3 (-1.7, -0.9)	-0.4 (-0.8, 0.1)	-0.2 (-0.9, 0.6)	0.01
Short-distance	-2.1 (-2.8, -1.4)	0.7 (0.2, 1.3)	<0.001	-1.1 (-1.6, -0.6)	-0.8 (-1.3, -0.3)	-0.2 (-1.1, 0.7)	0.56
Long-distance	-3.2 (-3.9, -2.4)	-3.0 (-3.6, -2.4)	0.67	-2.9 (-3.4, -2.3)	-2.7 (-3.3, -2.1)	-3.7 (-4.8, -2.7)	0.16
Irruptive	-0.04 (-0.3, 0.2)	-0.2 (-0.4, 0.1)	0.11	-0.6 (-0.8, -0.5)	0.1 (-0.2, 0.2)	0.3 (-0.1, 0.6)	<0.001
Departure from random for abundance							
All species	1.2 (-4.1, 6.6)	-5.3 (-9.6, -0.9)	0.13	-5.7 (-9.5, 1.9)	-1.2 (-5.5, 3.0)	0.8 (-6.5, 8.1)	0.09
Edge	-4.7 (-6.6, -2.9)	1.4 (-0.1, 2.9)	<0.001	0.5 (-0.8, 1.8)	-2.8 (-4.3, -1.4)	-2.6 (-5.1, -0.1)	0.05
Edge-interior	-0.7 (-3.0, 1.7)	-2.3 (-4.2, -0.4)	0.68	-2.2 (-3.8, -0.5)	0.4 (-1.5, 2.2)	-2.7 (-5.8, 0.5)	0.10
Interior	6.6 (3.4, 9.8)	-4.3 (-7.0, 1.8)	0.003	-4.0 (-6.2, -1.7)	1.2 (-1.3, 3.8)	6.1 (1.7, 10.5)	0.005
Resident	0.6 (-0.6, 1.8)	-0.5 (-1.6, 0.5)	0.34	-1.9 (-2.7, -1.0)	0.7 (-0.3, 1.6)	1.3 (-0.4, 2.9)	0.01
Short-distance	0.1 (-1.7, 1.8)	1.8 (0.4, 3.2)	0.54	-1.4 (-2.6, -0.2)	0.3 (-1.1, 1.7)	3.8 (1.5, 6.2)	0.01
Long-distance	-0.5 (-3.8, 2.7)	-6.6 (-9.2, -3.9)	0.07	-0.3 (-2.6, 2.0)	-3.8 (-6.4, -1.3)	-6.5 (-10.9, -2.0)	0.54
Irruptive	1.1 (-0.2, 2.5)	0.1 (-1.1, 1.1)	0.10	-2.2 (-3.2, 1.2)	1.6 (0.5, 2.7)	2.3 (0.4, 4.1)	<0.001

0.02), long-distance ($P < 0.001$), and possibly irruptive birds ($P = 0.08$). For the most part, variation in abundance among years was consistent among landscapes. However, for edge ($P = 0.08$), interior ($P = 0.06$), and resident birds ($P = 0.07$) there was a suggestion that differences in abundance between landscapes were different between years.

In both landscapes combined, 79 bird species were detected. Many (38%) were detected at less than 5% of sites and were not analyzed individually (Table 2). A large portion (37%) of the 49 species examined did not differ in occurrence from what would have been expected if birds were randomly distributed between landscapes (Table 3). Least Flycatcher (*Empidonax minimus*), Philadelphia Vireo (*Vireo philadelphicus*), American Crow (*Corvus brachyrhynchos*), House Wren (*Troglodytes aedon*), American Robin (*Turdus migratorius*), Cedar Waxwing (*Bombycilla cedrorum*), Clay-colored Sparrow (*Spizella pallida*), Song Sparrow (*Melospiza melodia*), Brown-headed Cowbird (*Molothrus ater*), and American Goldfinch (*Carduelis tristis*) were more common than expected in the fragmented landscape (Table 2). Conversely, Yellow-bellied Sapsucker (*Sphyrapicus varius*), Pileated Woodpecker (*Dryocopus pileatus*), Gray Jay (*Perisoreus canadensis*), Brown Creeper (*Certhia americana*), Red-breasted Nuthatch (*Sitta canadensis*), Winter Wren (*Troglodytes troglodytes*), Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Black-throated Green Warbler (*Dendroica virens*), Bay-breasted Warbler (*Dendroica castanea*), Canada Warbler (*Wilsonia canadensis*), White-winged Crossbill (*Loxia leucoptera*), and Evening Grosbeak (*Coccothraustes vespertinus*) were significantly more common than expected in contiguous forest (Table 3).

The interaction between forest type and landscape was significant for three species. Ruby-crowned Kinglet (*Regulus calendula*) was more common in fragmented mixedwood stands than in contiguous forest ($P = 0.002$), while there was no difference between landscapes in white spruce ($P > 0.05$) or trembling aspen ($P > 0.05$). Ovenbird (*Seiurus aurocapillus*) was more common than expected in contiguous forest dominated by aspen than in aspen forest fragments ($P < 0.001$) and

mixedwoods ($P = 0.007$), whereas they were always less common than expected in white spruce. Cape May Warbler (*Dendroica tigrina*) was significantly more common in white spruce stands in contiguous forest than forest fragments ($P = 0.04$), whereas there was no difference between landscapes in mixedwoods ($P > 0.05$) or trembling aspen ($P > 0.05$). Finally, Swainson's Thrush (*Catharus ustulatus*) was more common than expected in pure aspen stands in contiguous forest than in forest fragments ($P = 0.03$), whereas there was no difference in mixedwoods ($P > 0.05$) or white spruce stands ($P > 0.05$).

Half the species (51%) showed a preference for a particular forest type (Table 3). Red-eyed Vireo (*Vireo olivaceus*), Hermit Thrush (*Catharus guttatus*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Black and White Warbler (*Mniotilta varia*), Ovenbird, American Redstart (*Setophaga ruticilla*), White-throated Sparrow (*Zonotrichia albicollis*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Brown-Headed Cowbird were more common than expected in trembling aspen stands (Table 3). In contrast, American Crow, Boreal Chickadee (*Podiceps hudsonicus*), Ruby-crowned Kinglet, Cape May Warbler, Yellow-rumped Warbler (*Dendroica coronata*), Bay-breasted Warbler, Dark-eyed Junco (*Junco hyemalis*), and Pine Siskin (*Carduelis pinus*) were more common than expected in pure white spruce stands (Table 3). Blue-headed Vireo (*Vireo solitarius*), Gray Jay, Red-breasted Nuthatch, Blackburnian Warbler (*Dendroica fusca*), Black-throated Green Warbler (*Dendroica virens*), Chipping Sparrow (*Spizella passerina*), and White-winged Crossbill, and were more common than expected in white spruce and mixedwoods relative to trembling aspen (Table 3). The occurrence of 12 species was influenced by year (Table 3). However, annual variation was consistent among landscapes, as year interacted with landscape strongly for only two species (Table 3). Boreal Chickadee was significantly more common in contiguous forest in 1993 only, while Ruby-crowned Kinglet was significantly more common in forest fragments in 1995 only.

Factors influencing avian communities in the fragmented landscape.—The departure from random for species richness was not cor-

TABLE 2. Probability that the abundance of individual species was influenced by forest fragment size, forest cover within 5 km of site, forest type, and year, more than would be expected if individuals were randomly distributed. The slope of significant relationships is indicated as positive (+) or negative (-). All species detected in study area are shown.

Common name	Scientific name	Edge sensitivity ^a	Migratory strategy ^b	Size	Cover	Forest	Year	S × C
Species more common in small fragments or areas with low local forest cover								
American Crow	<i>Corvus brachyrhynchos</i>	EI	S	NS	0.10 ⁻	0.01	NS	NS
House Wren	<i>Troglodytes aedon</i>	E	S	NS	NS	0.06	NS	0.03 ⁺
Ruby-crowned Kinglet	<i>Regulus calendula</i>	I	S	NS	0.03 ⁻	0.001	NS	NS
American Robin	<i>Turdus migratorius</i>	E	S	NS	NS	NS	NS	0.09
Clay-colored Sparrow	<i>Spizella pallida</i>	E	L	0.07	0.007 ⁻	NS	NS	0.06
Song Sparrow	<i>Melospiza melodia</i>	E	S	0.008 ⁺	0.09 ⁻	0.009	0.03	NS
Species more common in large fragments or areas with high local forest cover within 5 km								
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	EI	S	0.01 ⁺	NS	NS	NS	NS
Hairy Woodpecker	<i>Picoides villosus</i>	I	R	0.03 ⁺	NS	NS	NS	NS
Black-capped Chickadee	<i>Podiceps atricapillus</i>	EI	R	0.07 ⁺	NS	NS	NS	0.04 ⁺
Cedar Waxwing	<i>Bombycilla cedrorum</i>	E	S	0.09 ⁺	NS	0.06	NS	NS
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	E	L	NS	0.02 ⁺	0.01	NS	NS
Mourning Warbler	<i>Oporornis philadelphia</i>	E	L	NS	0.07 ⁺	NS	NS	NS
Connecticut Warbler	<i>Oporornis agilis</i>	I	L	0.009 ⁺	NS	NS	NS	NS
Ovenbird	<i>Seiurus aurocapillus</i>	I	L	0.004 ⁺	0.002 ⁺	NS	NS	0.04 ⁺
American Redstart	<i>Setophaga ruticilla</i>	I	L	0.01 ⁺	0.001 ⁺	0.003	NS	NS
White-throated Sparrow	<i>Zonotrichia albicollis</i>	E	S	0.03 ⁺	NS	0.04	0.04	NS
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	EI	L	0.007 ⁺	NS	0.05	NS	NS
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	EI	Ir	0.07 ⁺	NS	NS	NS	NS
Species more common in large fragments with low forest cover within 5 km								
Red-breasted Nuthatch	<i>Sitta canadensis</i>	I	R	NS	0.02 ⁻	0.007	NS	0.008 ⁻
Cape May Warbler	<i>Dendroica tigrina</i>	I	L	NS	NS	0.02	NS	0.002 ⁻
Yellow-rumped Warbler	<i>Dendroica coronata</i>	I	S	NS	0.04 ⁻	0.001	NS	0.07 ⁻
Blackburnian Warbler	<i>Dendroica fusca</i>	I	L	NS	0.01	0.003	NS	0.004 ⁻
Chipping Sparrow	<i>Spizella passerina</i>	E	L	NS	0.008 ⁻	0.03	0.02	0.03
Dark-eyed Junco	<i>Junco hyemalis</i>	E	S	NS	NS	0.002	NS	0.02 ⁻
Pine Siskin	<i>Carduelis pinus</i>	EI	Ir	NS	0.02 ⁻	0.01	NS	0.009 ⁻
Species randomly distributed within fragmented landscape								
Ruffed Grouse	<i>Bonasa umbellus</i>	EI	R	NS	NS	NS	NS	NS
Pileated Woodpecker	<i>Dryocopus pileatus</i>	EI	R	NS	NS	NS	NS	NS
Least Flycatcher	<i>Empidonax minimus</i>	E	L	NS	NS	0.05	NS	NS

TABLE 2. CONTINUED

Common name	Scientific name	Edge sensitivity ^a	Migratory strategy ^b	Size	Cover	Forest	Year	S × C
Blue-headed Vireo	<i>Vireo solitarius</i>	I	L	NS	NS	0.001	NS	NS
Red-eyed Vireo	<i>Vireo olivaceus</i>	EI	L	NS	NS	0.06	NS	NS
Philadelphia Vireo	<i>Vireo philadelphicus</i>	EI	L	NS	NS	0.05	NS	NS
Blue Jay	<i>Cyanocitta cristata</i>	EI	R	NS	NS	NS	NS	NS
Common Raven	<i>Corvus corax</i>	EI	R	NS	NS	NS	NS	NS
Boreal Chickadee	<i>Poecile hudsonicus</i>	I	R	NS	NS	NS	NS	NS
Hermit Thrush	<i>Catharus guttatus</i>	I	S	NS	NS	NS	NS	NS
Tennessee Warbler	<i>Vermivora peregrina</i>	EI	L	NS	NS	NS	NS	NS
Black-and-white Warbler	<i>Mniotilta varia</i>	I	L	NS	NS	NS	NS	NS
Yellow Warbler	<i>Dendroica petechia</i>	E	L	NS	NS	NS	NS	NS
Canada Warbler	<i>Wilsonia canadensis</i>	I	L	NS	NS	NS	NS	NS
Brown-headed Cowbird	<i>Molothrus ater</i>	E	S	NS	NS	0.003	0.08	NS
White-winged Crossbill	<i>Loxia leucoptera</i>	EI	Ir	NS	NS	NS	NS	NS
American Goldfinch	<i>Carduelis tristis</i>	E	S	NS	NS	NS	0.07	NS
Species rare in fragmented landscape and not tested statistically								
Mourning Dove	<i>Zenaidura macroura</i>	E	S					
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	E	L					
Northern Flicker	<i>Colaptes auratus</i>	EI	S					
Downy Woodpecker	<i>Picoides pubescens</i>	EI	R					
Three-toed Woodpecker	<i>Picoides tridactylus</i>	I	R					
Black-backed Woodpecker	<i>Picoides arcticus</i>	I	R					
Olive-sided Flycatcher	<i>Contopus borealis</i>	EI	L					
Western Wood-Pee-wee	<i>Contopus sordidulus</i>	EI	L					
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	I	L					
Alder Flycatcher	<i>Empidonax minimus</i>	E	L					
Eastern Phoebe	<i>Sayornis phoebe</i>	EI	S					
Warbling Vireo	<i>Vireo gilvus</i>	E	L					
Gray Jay	<i>Perisoreus canadensis</i>	EI	R					
Black-billed Magpie	<i>Pica pica</i>	E	R					
Tree Swallow	<i>Tachycineta bicolor</i>	EI	L					
Barn Swallow	<i>Hirundo rustica</i>	EI	S					
Brown Creeper	<i>Certhia americana</i>	I	S					
White-breasted Nuthatch	<i>Sitta carolinensis</i>	I	R					
Winter Wren	<i>Troglodytes troglodytes</i>	I	S					
Golden-crowned Kinglet	<i>Regulus satrapa</i>	I	S					

TABLE 2. CONTINUED

Common name	Scientific name	Edge sensitivity ^a	Migratory strategy ^b	Size	Cover	Forest	Year	S × C
Veery	<i>Catharus fuscescens</i>	I	L					
Swainson's Thrush	<i>Catharus ustulatus</i>	I	L					
Magnolia Warbler	<i>Dendroica magnolia</i>	I	L					
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	I	L					
Black-throated Green Warbler	<i>Dendroica virens</i>	I	L					
Bay-breasted Warbler	<i>Dendroica castanea</i>	I	L					
Wilson's Warbler	<i>Wilsonia pusilla</i>	I	L					
Northern Waterthrush	<i>Seiurus noveboracensis</i>	I	L					
Western Tanager	<i>Piranga ludoviciana</i>	I	L					
Savanna Sparrow	<i>Passerculus sandwichensis</i>	E	S					
Lincoln's Sparrow	<i>Melospiza lincolni</i>	E	L					
Vesper Sparrow	<i>Pooecetes gramineus</i>	E	S					
Common Grackle	<i>Quiscalus quiscula</i>	E	S					
Baltimore Oriole	<i>Icterus galbula</i>	E	L					
Purple Finch	<i>Carpodacus purpureus</i>	EI	S					
Red Crossbill	<i>Loxia curvirostra</i>	I	Ir					
Pine Grosbeak	<i>Pinicola enucleator</i>	E	Ir					

^a E = edge, I = interior, EI = edge-interior.

^b R = resident, S = short-distance migrant, L = long-distance migrant, Ir = irruptive.

TABLE 3. Proportion of sites where departure from expected was greater than zero in each landscape and forest stand type. Results of logistic regression models for all parameters examined are also given. Parameters with NS were not selected in the model.

Species	Landscape			Forest stand type				Year	L × Y	L × F
	For-est	Frag-ments	P	TA	Mix	WS	P	P	P	P
Species more common than expected in fragmented landscape										
Least Flycatcher	9	22	0.01	26	6	6	NS	NS	NS	NS
Philadelphia Vireo	4	27	0.02	30	6	0	0.005	NS	NS	NS
American Crow	7	22	0.01	9	20	44	0.002	NS	NS	NS
House Wren	0	19	0.02	19	4	6	NS	NS	NS	NS
American Robin	6	27	0.003	24	14	17	NS	NS	NS	NS
Cedar Waxwing	11	22	0.002	15	20	28	NS	0.09	0.07	NS
Clay-colored Sparrow	0	17	0.02	9	12	22	NS	NS	NS	NS
Song Sparrow	0	43	0.004	39	8	28	NS	0.03	0.10	NS
Brown-headed Cowbird	4	40	0.001	38	12	6	0.001	0.04	NS	NS
American Goldfinch	0	35	0.002	23	18	39	NS	0.60	NS	NS
Species more common than expected in contiguous forest										
Yellow-b. Sapsucker	26	12	0.03	14	22	17	NS	0.07	NS	NS
Pileated Woodpecker	20	3	0.001	7	10	17	NS	NS	NS	NS
Gray Jay	26	3	0.001	2	26	11	0.005	NS	NS	NS
Brown Creeper	33	0	0.001	7	16	22	NS	NS	NS	NS
Red-breasted Nuthatch	35	13	0.06	10	36	33	0.002	0.05	NS	NS
Winter Wren	28	19	0.002	3	16	6	NS	NS	0.08	NS
Swainson's Thrush	46	2	0.001	7	32	28	NS	NS	NS	0.001
Tennessee Warbler	57	5	0.001	17	32	22	NS	0.05	NS	NS
Magnolia Warbler	35	1	0.001	8	18	22	NS	NS	NS	NS
Black-thr. Green Warbler	39	0	0.001	7	22	22	0.06	NS	NS	NS
Bay-breasted Warbler	33	1	0.001	2	22	33	0.001	NS	NS	NS
Canada Warbler	20	4	0.001	13	6	0	NS	NS	NS	NS
Ovenbird	61	18	NS	41	28	0	0.001	NS	NS	0.001
White-winged Crossbill	24	7	0.009	5	22	22	0.03	NS	NS	NS
Evening Grosbeak	24	3	0.001	4	18	17	NS	NS	NS	NS
Species randomly distributed among landscapes										
Ruffed Grouse	13	33	NS	28	26	17	NS	0.003	NS	NS
Hairy Woodpecker	20	7	NS	12	10	11	NS	0.03	NS	NS
Blue-headed Vireo	22	21	NS	8	36	50	0.001	0.08	NS	NS
Red-eyed Vireo	30	42	NS	50	26	11	0.002	NS	NS	NS
Blue Jay	9	15	NS	10	20	11	NS	NS	NS	NS
Common Raven	22	14	NS	14	20	22	NS	NS	NS	NS
Black-capped Chickadee	15	17	NS	15	18	17	NS	NS	NS	NS
Boreal Chickadee	20	5	NS	2	18	27	0.002	NS	0.006	NS
Ruby-crowned Kinglet	24	36	NS	13	50	78	0.001	NS	0.006	0.02
Hermit Thrush	24	22	NS	29	16	6	0.01	NS	NS	NS
Chestnut-sided Warbler	20	30	NS	41	10	0	0.002	NS	NS	NS
Cape May Warbler	26	10	NS	2	30	44	0.001	NS	NS	0.04
Yellow-rumped Warbler	37	21	NS	8	48	67	0.001	NS	NS	NS
Black-and-White Warbler	11	19	NS	24	6	6	0.02	NS	NS	NS
Blackburnian Warbler	24	18	NS	8	36	39	0.001	NS	NS	NS
Yellow Warbler	2	10	NS	12	0	0	NS	NS	NS	NS
Mourning Warbler	17	30	NS	30	24	6	NS	NS	NS	NS
Connecticut Warbler	19	14	NS	20	14	0	NS	NS	NS	NS
American Redstart	15	27	NS	39	2	0	0.004	NS	NS	NS
Chipping Sparrow	30	25	NS	13	42	50	0.002	0.005	NS	NS
White-throated Sparrow	28	19	NS	32	10	6	0.002	0.04	NS	NS
Dark-eyed Junco	7	10	NS	3	8	44	0.001	NS	NS	NS
Rose-breasted Grosbeak	20	28	NS	37	14	0	0.02	NS	NS	NS
Pine Siskin	32	15	NS	4	36	61	0.001	NS	NS	NS

related with fragment size for all species ($r = -0.01$, $P > 0.05$), edge-interior ($r = 0.18$, $P > 0.05$), interior ($r = 0.14$, $P > 0.05$), short-distance migrants ($r = -0.17$, $P > 0.05$), long-distance migrants ($r = -0.01$, $P > 0.05$), or irruptive species ($r = 0.08$, $P > 0.05$). The departure from random for edge species was negatively correlated with forest fragment size ($r = -0.27$, $P = 0.01$), while resident species were positively correlated with forest fragment size ($r = 0.22$, $P = 0.05$). The departure from random for richness of long-distance migrants was positively correlated with the proportion of forest cover within 5 km ($r = 0.22$, $P = 0.03$). Forest type had a significant influence on the departure from random for the richness of irruptives ($P < 0.001$), residents ($P = 0.02$), and interior species ($P = 0.03$). Annual variation in the departure from random was significant for richness of all species ($P < 0.001$), edge ($P < 0.001$), edge-interior ($P < 0.001$), residents ($P = 0.04$), short-distance migrants ($P = 0.04$), and long-distance migrant species ($P < 0.001$).

The departure from random for abundance was positively correlated with forest fragment size for all birds ($r = 0.58$, $P < 0.001$), edge-interior ($r = 0.47$, $P < 0.001$), interior ($r = 0.52$, $P < 0.001$), resident ($r = 0.28$, $P = 0.01$), long-distance ($r = 0.45$, $P < 0.001$), and irruptive birds ($r = 0.30$, $P = 0.02$). The departure from random for abundance of edge species ($r = 0.18$, $P > 0.05$) and short-distance migrants ($r = 0.11$, $P > 0.05$) was not correlated with forest fragment size. Long-distance migrant ($r = 0.36$, $P = 0.005$) and interior bird ($r = 0.26$, $P = 0.02$) abundance was positively correlated with the percentage of forest cover within 5 km. Annual variation in the departure from random was significant for total abundance of all species ($P < 0.001$), edge ($P < 0.001$), edge-interior ($P < 0.001$), interior ($P = 0.05$), residents ($P = 0.03$), short-distance migrants ($P = 0.004$), and long-distance migrant birds ($P < 0.001$). The type of forest influenced the departure from random for edge ($P = 0.01$), resident ($P = 0.03$), short-distance migrant ($P = 0.03$), long-distance migrant ($P < 0.001$), and irruptive birds ($P = 0.004$).

Of the 42 species examined in the fragmented landscape, 40% did not differ in abundance from what was expected if individuals

were distributed randomly and showed no area or isolation sensitivity. American Crow, Ruby-crowned Kinglet, Clay-colored Sparrow, and Song Sparrow were negatively correlated with forest cover within 5 km. Clay-colored Sparrow and Song Sparrow were more common than expected in small forest fragments (Table 2). The departure from random was positively correlated with forest fragment size for Yellow-bellied Sapsucker, Hairy Woodpecker, Black-capped Chickadee (*Poecile atricapillus*), Cedar Waxwing, Connecticut Warbler (*Oporornis agilis*), Ovenbird, American Redstart, White-throated Sparrow, Rose-breasted Grosbeak, and Evening Grosbeak (Table 2). Chestnut-sided Warbler, Mourning Warbler (*Oporornis philadelphia*), Ovenbird, and American Redstart were more common in areas with higher local forest cover (Table 2). The departures from expected for Red-breasted Nuthatch, Cape May Warbler, Yellow-rumped Warbler, Blackburnian Warbler, Chipping Sparrow, Dark-eyed Junco, and Pine Siskin were significantly correlated with the interaction between size and local forest cover. All of these species were more common than expected in mature white spruce stands that were large but isolated. Year was a significant predictor of the departure from random for Chipping Sparrow, Song Sparrow, White-throated Sparrow, Brown-headed Cowbird, and American Goldfinch (Table 2). In total, 21 species showed a preference for a particular forest type in the fragmented landscape (Table 2).

Nest success.—We located 67 nests from eight species in the fragmented landscape and 56 nests from seven species in contiguous forest. The majority of nests located were Ovenbird (59%), followed by Hermit Thrush (13%), Chipping Sparrow (11%), White-throated Sparrow (7%), and a one or two nests each of Red-eyed Vireo, Tennessee Warbler, Yellow-rumped Warbler, Mourning Warbler, Connecticut Warbler, and American Redstart. Daily nest survival was significantly lower in the fragmented landscape (0.960 ± 0.007) than in contiguous forest (0.979 ± 0.005 ; $P = 0.02$). Cowbird parasitism was more common in the fragmented landscape where 19% of nests were parasitized whereas no nests were parasitized in contiguous forest ($\chi^2 = 18.8$, $P < 0.001$).

DISCUSSION

Species richness was higher in the fragmented landscape than in contiguous forest. The increase in species richness with fragmentation was primarily due to the addition of several short-distance migrants that were associated with edge habitats. In contrast, long-distance migrant and resident species were present in both landscapes and no difference in species richness was observed for these groups. The total abundance of long-distance migrants and interior species was higher in contiguous forest than expected, suggesting that the density of many of these species was higher in contiguous forest than in forest fragments. These results indicate that boreal forest birds suffer similar effects from habitat fragmentation caused by agriculture as do birds in other fragmented landscapes.

Bird communities in forest fragments in the boreal forest are not merely random samples from the species pool at the regional scale (Connor and McCoy 1979, Coleman et al. 1982, Møller 1987). Many species were more common in large fragments or in areas that were less isolated than would be expected if individuals were randomly distributed across the landscape (Freemark and Collins 1992, Hinsley et al. 1995). Species such as Tennessee Warbler, Magnolia Warbler, Black-throated Green Warbler, Bay-breasted Warbler, and Canada Warbler were all relatively common in contiguous forest, but were rare in the agricultural landscape. In particular, Tennessee Warbler was present at 81% of all contiguous forest sites but was present at only 26% of sites in the agricultural landscape. Clearly, non-random mechanisms influence the abundance and frequency of certain species between and within landscapes.

Many species in the boreal forest showed a preference for a specific forest type. In particular, white spruce and mixedwood stands supported very different bird communities than pure trembling aspen stands (Hobson and Bayne, in press). Aspen stands in the boreal forest of Saskatchewan usually have a relatively simple vertical structure, consisting of a dense 1–3 m shrub layer and the canopy. In contrast, white spruce and mixedwood stands are structurally more diverse, with greater plant diversity and structural heterogeneity at

the shrub, subcanopy, and canopy levels (Hobson and Bayne, in press). As a consequence, mixedwood and white spruce stands have more nesting and foraging niches and tend to support more avian species than pure aspen stands. Regardless, differences among landscapes were usually similar among forest types indicating that the effects of forest fragmentation occur across a broad range of vegetation types.

In North America, lower densities of forest birds in forest fragments have typically been associated with processes related to differential reproductive success. Typically, nesting and pairing success are lower near edges and in small patches compared with forest interiors (Villard et al. 1993, Van Horne et al. 1995, Hagan et al. 1996). Although we did not have sufficient data to test for area effects on nest predation, our results suggest that predation and brood parasitism are higher in forest fragments than in contiguous forest. Whether increased nest predation is the cause of differences in avian community structure in the boreal forest is unclear. We have found that Ovenbirds in small forest fragments that were not successful at breeding are less likely to return to a site than successful breeders (Bayne 2000). In addition, Ovenbirds have much lower apparent annual survival in small forest fragments (34%) than in contiguous forest (62%, $P = 0.02$) which we attributed to increased dispersal from areas of high nest predation (Bayne 2000).

Andrén (1994) argued that landscape context may be a particularly important predictor of the severity of fragmentation effects. Our work supports this hypothesis; we found that area-sensitivity depended on the amount of forested land within 5 km. We found that a number of species associated with white spruce were area-sensitive, but only when fragments were isolated. Small patches that are close to other forest patches may be more suitable to forest birds than large isolated fragments for a variety of reasons. Resident species may be less likely to colonize isolated patches because of difficulties in dispersing across an open landscape (Matthysen and Currie 1996). For long-distance and short-distance migrants, nest predation may be more intense in isolated fragments than in small fragments in a landscape with higher local for-

est cover. Predation rates are often highly dependent on the amount of forested land in the landscape, probably because generalist predators typical of fragmented landscapes react more to landscape composition than to local fragment characteristics such as fragment size (Oehler and Litvatis 1996, Bayne and Hobson 1997, Donovan et al. 1997). Finally, birds may be able to move between patches in less isolated areas to obtain sufficient resources and may in fact defend territories in different patches (Rail et al. 1997).

In North America, most studies examining the effects of forest fragmentation on breeding bird assemblages have been conducted in landscapes that have been fragmented for long periods and that are considerable distances from large tracts of contiguous forest. We found little evidence that boreal forest birds considered area sensitive elsewhere are predisposed to coping with anthropogenic fragmentation any better than species occurring predominately in more southern forests. However, in boreal forest fragments surrounded by agriculture, American Redstart, Ovenbird, Hermit Thrush, and Connecticut Warbler were found in fragments considerably smaller than those 200 km south of our study area (Johns 1993). This suggests that birds may demonstrate a differential response to forest fragmentation, and particularly their choice of minimum fragment size, depending on distance from contiguous forest. However, Johns (1993) did not take into account the importance of random placement. The larger area requirements of long-distance migrants in the Aspen Parkland of Saskatchewan relative to the Boreal Forest may also be due to the fact that birds are regionally less abundant in the Aspen Parkland (Brown 1984).

Our recent examination of LANDSAT imagery for the southern boreal transition zone in Saskatchewan (i.e., that region of the Boreal Plains ecozone south of the commercial forest boundary) revealed that nearly 75% of this area has been cleared for agriculture since European settlement in the early 1900s. The consequences of the change from contiguous boreal forest to a landscape highly fragmented by agriculture have been the northern movement of avifauna associated with more open or parkland habitat, such as Clay-colored Sparrow, House Wren, American Goldfinch,

and Brown-headed Cowbird. These species may benefit initially by the creation of a more open landscape containing boreal forest fragments. However, several species more typical of the Boreal Plains Ecozone, namely those resident and long-distance migrant species identified here, have lost a considerable portion of their habitat, and several of these species show some sensitivity to forest fragment size and isolation. These fragments may ultimately function as sink habitat for some species (Bayne 2000). Species of particular concern include Tennessee Warbler, Magnolia Warbler, Bay-breasted Warbler, and Black-throated Green Warbler. All of these species occurred less frequently than expected in the fragmented landscape. In addition, these species require mature to old mixedwood and white spruce forests that are currently under intense pressure from forestry companies, both in the agricultural and commercial forestry zones of the boreal forest.

We examined only the effects of fragmentation of boreal forest by agriculture, a process evident throughout the entire portion of privately owned or Crown leased lands in the Boreal Plains ecozone of Saskatchewan and largely typical of similar areas in Alberta and Manitoba. Fragmentation of the remaining boreal forest in these provinces of western Canada is also occurring through commercial forestry (Cumming et al. 1994, Stelfox 1995). Unlike fragmentation by agriculture, gaps created by forestry are usually temporary, and therefore may have less effect on avian communities in the long term (Schmiegelow et al. 1996, Drolet and Desrochers 1999). Harvested landscapes retain a forested matrix that may prevent the invasion of generalist predators that are adapted to human-dominated landscapes (Andr n 1995). Further studies are required to examine the long-term consequences of habitat loss and fragmentation on forest birds and other wildlife in both agricultural and commercial forest landscapes in western Canada. This will be particularly important as contiguous forests that might act as population sources for most boreal forest breeding birds become proportionately less available on the landscape.

ACKNOWLEDGMENTS

E. Cumming and S. van Wilgenburg conducted bird censuses. S. van Wilgenburg also assisted with LAND-

SAT and GIS interpretations. Funding was provided by the Canadian Wildlife Service, Prince Albert National Park, Prince Albert Model Forest (Project 211) and a federal-Saskatchewan Partnership Agreement in Forestry (Project CS 5006). Personal support to E.M.B. was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) post-graduate scholarship, and a graduate fellowship from the University of Saskatchewan and the Canadian Wildlife Service. We thank Prince Albert National Park for allowing us to conduct surveys and for assisting with logistical support. Thanks also to the land owners who provided us access to their lands. P. Porneluzi, J. Faaborg, W. A. Montevecchi, K. Lewis, and M. Darveau provided helpful comments on earlier versions of the manuscript.

LITERATURE CITED

- AMBUEL, B. AND S. A. TEMPLE. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057–1068.
- ANDRÉN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366.
- ANDRÉN, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pp. 225–255 in *Mosaic landscapes and ecological processes* (L. Hansson, L. Fahrig, and G. Merriam, Eds.). Chapman and Hall, New York.
- ANDRÉN, H. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. *Oikos* 76:235–242.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. *Curr. Ornithol.* 7:1–57.
- ASKINS, R. A., M. J. PHILBRICK, AND D. S. SUGENO. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biol. Conserv.* 39:129–152.
- BAYNE, E. M. 2000. Effects of forest fragmentation on the demography of Ovenbirds (*Seiurus aurocapillus*) in the Boreal forest. Ph.D. thesis. Univ. of Saskatchewan, Saskatoon.
- BAYNE, E. M. AND K. A. HOBSON. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conserv. Biol.* 11:1418–1429.
- BLAKE, J. AND J. R. KARR. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* 68:1724–1734.
- BLONDEL, J., C. FERRY, AND B. FROCHOT. 1970. La methode des indices ponctuels d'abundance (ipa) ou des releves d'avifaune par "stations d'ecoute" *Alauda* 38:55–71.
- BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124:255–279.
- BURKE, D. M. AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96–104.
- BURNHAM, K. P. AND D. R. ANDERSON. 1998. Model selection and inference—a practical information theoretic approach. Springer-Verlag, New York.
- COLEMAN, B. D., M. A. MARES, M. R. WILLIG, AND Y. H. HSIEH. 1982. Randomness, area, and species richness. *Ecology* 63:1121–1133.
- COLWELL, R. K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. Version 5. URL = <http://viceroy.eeb.uconn.edu/estimates>
- CONNOR, E. F. AND E. D. MCCOY. 1979. The statistics and biology of the species-area relationship. *Am. Nat.* 113:791–833.
- CUMMING, S. G., P. J. BURTON, S. PRAHACS, AND M. R. GARLAND. 1994. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: a simulation study. *For. Ecol. Manage.* 68:281–302.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075.
- DROLET, B. AND A. DESROCHERS. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *Condor* 101:699–704.
- FAABORG, J., F. R. THOMPSON, III, S. ROBINSON, T. M. DONOVAN, D. R. WHITEHEAD, AND J. D. BRAUN. 1998. Understanding fragmented Midwestern landscapes: the future. Pp. 193–207 in *Avian conservation: research and management* (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, D.C.
- FREEMARK, K. E. AND B. COLLINS. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pp. 443–454 in *Ecology and conservation of Neotropical migrants* (D. W. Johnston, Ed.). Smithsonian Institution Press, Washington, D.C.
- FREEMARK, K. E. AND H. G. MERRIAM. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biol. Conserv.* 36:115–141.
- HAAS, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* 115:929–936.
- HAGAN, J. M., W. M. VANDER HAEGEN, AND P. S. MCKINLEY. 1996. The early development of forest fragmentation effects on birds. *Conserv. Biol.* 10:188–202.
- HAILA, Y., I. K. HANSKI, AND S. RAIVIO. 1993. Turnover of breeding birds in small forest fragments: the "sampling" colonization hypothesis corroborated. *Ecology* 74:714–725.
- HENSLER, G. L. AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bull.* 93:42–53.
- HINSLEY, S. A., P. E. BELLAMY, I. NEWTON, AND T. H. SPARKS. 1995. Habitat and landscape factors influencing the prescience of individual breeding bird

- species in woodland fragments. *J. Avian Biol.* 26: 94–104.
- HINSLEY, S. A., P. E. BELLAMY, I. NEWTON, AND T. H. SPARKS. 1996. Influence of population size and woodland area on bird distributions in small woods. *Oecologia* 105:100–106.
- HOBSON, K. A. AND E. M. BAYNE. Breeding bird communities in boreal forests of western Canada: consequences of unmixing in the mixedwoods. *Condor* In press.
- HOOD, G. 2000. PopTools. Pest Animal Control CRC. Canberra, Australia.
- JAMES, F. C. AND S. RATHBUN. 1981. Rarefaction, relative abundance, and diversity of avian communities. *Auk* 98:785–800.
- JOHNS, B. W. 1993. The influence of grove size in bird species richness in aspen parkland. *Wilson Bull.* 105:256–264.
- KLEINBAUM, D. G., L. L. KUPPER, AND K. E. MULLER. 1988. Applied regression analysis and other multivariate methods. PWS-Kent Publishing Company, Chapel Hill, North Carolina.
- LYNCH, J. F. AND D. F. WHIGHAM. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biol. Conserv.* 28:287–324.
- MANLY, B. 1990. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York.
- MATTHYSEN, E. AND D. CURRIE. 1996. Habitat fragmentation reduces disperser success in juvenile Nuthatches *Sitta europaea*: evidence from patterns of territory establishment. *Ecography* 19:67–72.
- MCCOLLIN, D. 1993. Avian distribution patterns in a fragmented wooded landscape (North Humber-side, U.K.): the role of between-patch and within-patch structure. *Global Ecol. Biogeogr. Lett.* 3:48–62.
- MØLLER, A. P. 1987. Breeding birds in habitat patches: random distribution of species and individuals? *J. Biogeogr.* 14:225–236.
- NIEMI, G., J. HANOWSKI, P. HELLE, R. HOWE, M. MÖNKKÖNEN, L. VENIER, AND D. WELSH. 1998. Ecological sustainability of birds in boreal forests. *Conserv. Ecol.* 2(2):17. URL = <http://www.consecol.org/vol2/iss2/art17>
- OEHLER, J. D. AND J. A. LITVAITIS. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Can. J. Zool.* 74:2070–2079.
- OPDAM, P., G. RIJSDIJK, AND F. HUSTINGS. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biol. Conserv.* 34:333–352.
- RAIL, J. F., M. DARVEAU, A. DESROCHERS, AND J. HUOT. 1997. Territorial responses of boreal forest birds to habitat gaps. *Condor* 99:976–980.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildl. Monogr.* 103:1–34.
- ROBINSON, S. K., F. R. THOMPSON, III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- SAUER, J. R. AND T. C. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* 53:137–142.
- SCHMIEGELOW, F. K. A., C. MACHTANS, AND S. J. HANNON. 1996. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* 78:1914–1932.
- STELFOX, J. B. (Ed.). 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forest in Alberta. Alberta Environmental Centre, Vegreville, Alberta; Canadian Forest Service, Edmonton, Alberta.
- TEMPLE, S. A. AND B. A. WILCOX. 1986. Introduction: predicting effects of habitat patchiness and fragmentation. Pp. 261–262 in *Wildlife 2000* (J. Verner, M. L. Morrison, and C. J. Ralph, Eds.). Univ. of Wisconsin Press, Madison.
- VAN HORNE, M. A., R. M. GENTRY, AND J. FAABORG. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112: 98–106.
- VILLARD, M. -A., P. R. MARTIN, AND C. G. DRUMMOND. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110: 759–768.
- WALTERS, J. R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. Pp. 181–192 in *Avian conservation: research and management* (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, D.C.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125–205 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess and D. M. Sharpe, Eds.). Springer-Verlag, New York.